



# Voles and climate in Norway: Is the abundance of herbivorous species inversely related to summer temperature?

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## ABSTRACT

For several mammalian species, both population levels and distribution ranges are predicted to change due to changing habitat conditions caused by climate change. A general decrease in the amplitude of small rodent population cycles in northern Europe since the late 1980s has commonly been attributed to a lack of permanent snow cover during winter, or to unfavourable snow conditions. An alternative explanation is that increasing summer temperatures and an extended growing season are unfavourable for herbivorous rodents, by reducing the forage quality. If so, the negative effect should be stronger for the strictly herbivorous *Microtus* voles than for the herbivorous-granivorous *Myodes* voles. In a previous study small rodents were snap trapped in 22 regions in Norway during 1971–1979. We found that the trapping index of *Microtus* voles, but not *Myodes* voles, in this study was negatively related to summer temperatures. Both in this study and in a snap trapping study from 1994 to 2015, conducted in 13 study areas in Norway, the proportion of *Microtus* voles among voles captured was negatively related to summer temperatures. Summer temperature was a better predictor than snow depth, but both variables contributed significantly in multiple regression models. We conclude that summer temperature is likely to be a more important factor than snow cover for the population dynamics of herbivorous voles in northern Europe.

## 1. Introduction

Climate change is a global disturbance factor that may affect regional animal populations both directly and indirectly (Battisti et al., 2016). For several mammalian species, both population levels and distribution ranges are predicted to change due to changing habitat conditions caused by climate change (e.g. Bisi et al., 2015; Ancillotto et al., 2018; Mori et al., 2018). In northern Europe, the amplitude of small rodent population cycles has generally decreased since the late 1980s (Cornulier et al., 2013), although with recovery in recent years (Brommer et al., 2010; Magnusson et al., 2015; Wegge and Rolstad, 2018). Because multiannual rodent cycles have been most pronounced in areas with cold climate (Hansson and Henttonen, 1985), the decreasing amplitude may be linked to global warming. The main focus in explaining the “fading out” of vole cycles has been on unfavourable snow conditions (e.g. Aars and Ims, 2002; Korslund and Steen, 2006; Kausrud et al., 2008, but see Hoset et al., 2009; Johnsen et al., 2018). However, changing snow conditions can hardly explain why rodent cycles have “faded out” also in parts of northern Europe that never had

permanent snow cover in winter (Cornulier et al., 2013). Although a stable snow cover protects small rodents against freezing temperatures (Wegge, 1967; Reid and Krebs, 1996; McCafferty et al., 2003) and predators (Hansson and Henttonen, 1985), it is not a prerequisite for high winter survival and subsequent population peaks of small rodents (Selås, 2016a).

In Finland, vole population dynamics during 1970–2011 correlated better with the growing season than with winter conditions (Korpela et al., 2013). In the Czech Republic, the dampening amplitude of a cyclic field vole *Microtus agrestis* population was related to increased summer temperatures rather than changes in winter climate conditions (Gouveia et al., 2015). A negative relationship between cycle amplitude and temperature is known also for other cyclic herbivores, such as the snowshoe hare *Lepus americanus* (Yan et al., 2013) and the larch bud-moth *Zeiraphera diniana* (Johnson et al., 2010).

Food is a key factor for the performance and population dynamics of small rodents (Ylönen and Eccard, 2004; Von Blanckenhagen et al., 2007; Wereszczynska et al., 2007; Palo and Olsson, 2009; Haapakoski and Ylönen, 2013; Forbes et al., 2014a, b; Johnsen et al., 2016). In

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Fennoscandia, the decrease in cycle amplitude has been more pronounced for the field vole than for the sympatric bank vole *Myodes glareolus* (Brommer et al., 2010; Gorini et al., 2011; Khalil et al., 2016). An explanation for this difference could be that negative effects of warmer summers acting through reduced forage quality (e.g. Jonasson et al., 1986; Laine and Henttonen, 1987; Selås, 2000; White, 2011) are more detrimental for *Microtus* voles than for *Myodes* voles, the former being strictly herbivorous and the latter herbivorous-granivorous (Hansson, 1971a).

If *Microtus* voles are more negatively affected by warm summers than are *Myodes* voles, there should also be a spatial gradient in the *Microtus/Myodes* ratio, related to local summer temperatures. Hansson (1992) found that the number of field voles in forest clear-cuts increased northwards in Sweden, but he related this only to snow cover and winter severity. Here, we test the prediction that a stronger negative impact of warm summers on *Microtus* voles than on *Myodes* voles is reflected at a spatial scale by using data from snap trapping studies in different parts of Norway with different summer temperatures.

## 2. Material and methods

### 2.1. Study species

The five vole species included in our analyses are field vole, tundra vole *Microtus oeconomus*, bank vole, red vole *Myodes rutilus* and grey-sided vole *M. rufocanus*. Field vole, tundra vole and grey-sided vole have a wide distribution in Norway, but the latter two species do not occur at lower elevations in South Norway. The bank vole is restricted to South Norway and Nordland County and is substituted by the red vole farther north.

### 2.2. Study areas and trapping protocols 1971–1979

Christiansen (1973, 1983) snap-trapped voles in 22 forest districts, situated in the boreo-nemoral and boreal vegetation zones, each autumn during 1971–1979 (Table 1; Fig. 1a). In this period, vole cycles showed a relatively high degree of spatial synchrony in Norway, with marked peaks in 1972–74 and 1976–78. In each district, 144–432 snap traps were set out for two consecutive days in 4–14 study sites during

15–30 September, and the total number of *Microtus* and *Myodes* voles captured in each district ranged between 98 and 895 (Table 1).

The traps were put out in four main habitats (Fig. 1 in Christiansen, 1983): 1) reforestation in coniferous or mixed coniferous/deciduous forest, 2) reforestation in deciduous forest and shrub, 3) afforestation in abandoned fields, 4) afforestation on drained peat land. These habitats usually have a high dominance of grass and herbs and are thus regarded as suitable habitats for *Microtus* voles (Hansson, 1971b). In most districts, one or two habitats dominated, by covering more than 75% of the areas. Habitat 1 dominated in two districts (no. 5 and 9, Table 1), habitat 1 and 2 in ten districts (no. 1–4, 6–8, 16, 17 and 20), habitat 2 and 3 in six districts (no. 11–14, 21 and 22), habitat 4 in two districts (no. 10 and 18), and habitat 1 and 4 in one district (no. 19). In the remaining district (no. 15), habitat 3 covered 50% of the area, whereas the three remaining habitats were almost equally abundant.

Christiansen (1973, 1983) gave the approximate location for each of the 22 forest districts on a map, but he did not report mean elevation. However, upon request, Christiansen (pers. comm.) provided an estimate of mean elevation for his study sites in each of the 22 districts.

### 2.3. Study areas and trapping protocols 1994–2015

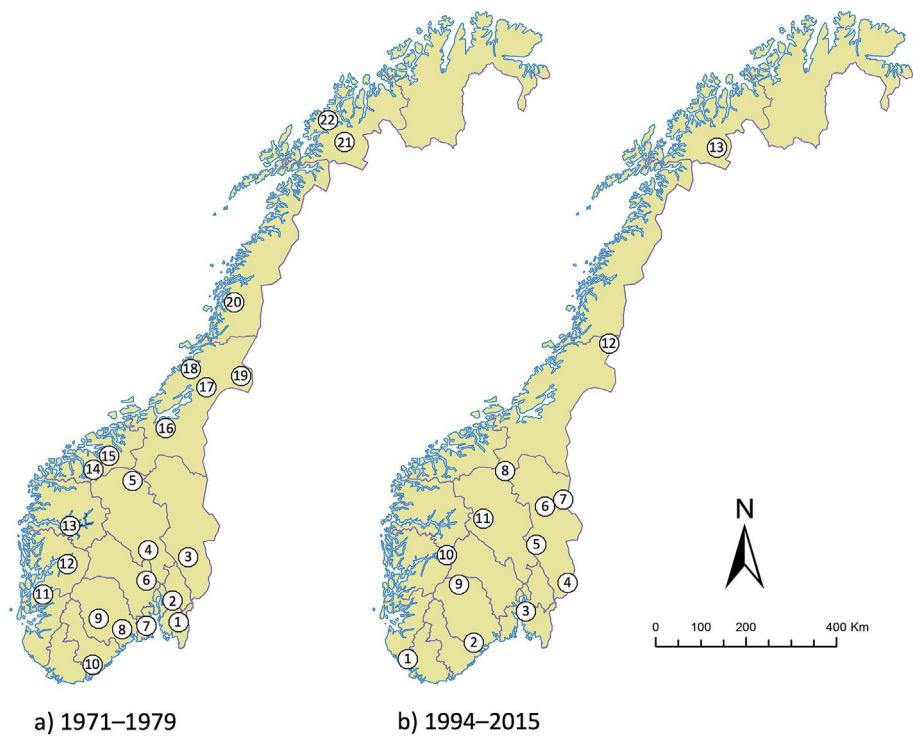
For the period 1994–2015, we used data from 13 study areas, mainly from the boreal vegetation zone, where relative vole numbers have been estimated by snap-trapping each autumn (Table 2, Fig. 1b). The annual number of trap-nights was c. 400 in most areas and years, except from areas 2, 5, 10 and 13 (Table 2), where the number was 1000–1500 in most years. Seven of the study areas are included in the Terrestrial Ecosystem Monitoring (TOV) conducted by the Norwegian Institute for Nature Research, who presents the results in annual reports (see Framstad, 2017). Permission for snap trapping was given by the Norwegian Environment Agency.

One study area (no. 10, Table 2) is situated in the low alpine area, where the vegetation consists of a mixture of dwarf shrubs, herbs, grasses, sedges, lichens and mosses. Common species are bilberry *Vaccinium myrtillus*, crowberry *Empetrum nigrum* and wavy hair-grass *Avenella flexuosa*. Nine study areas (no. 1, 6–9 and 11–13) are situated in boreal mountain forests, i.e. relatively open areas where the dominating plants in the field layer will depend more on soil type and

**Table 1**

Sampling districts in Norway where voles were snap-trapped in autumn during 1971–1979. Vole numbers are taken from Christiansen (1983), and mean altitude for each locality is estimated by E. Christiansen (pers. comm.). Dominating vegetation zone (Moen, 1999) is given as BN = boreo-nemoral, SB = southern boreal, MB = middle boreal, NB = northern boreal, A = alpine. The meteorological station used for calculating altitude-adjusted summer temperature is given for each district.

Sampling district	Mean altitude (m a.s.l.)	Latitude	Longitude	Number of voles trapped	Meteorological station and altitude (m a.s.l.)
1 Eidsberg (BN)	106	59.53	11.26	270	Håby 100
2 Enebakk (BN)	225	59.74	11.11	229	Ås 95
3 Stange/Vang (SB)	190	60.67	11.25	98	Ilseeng 182
4 Nordre land (SB)	350	60.83	10.11	282	Vest-Torpa 542
5 Dovre (MB)	600	61.97	9.30	131	Dombås 638
6 Ringerike (SB)	150	60.23	10.18	149	Høyby 140
7 Stokke (BN)	88	59.24	10.15	192	Horten 95
8 Skien (BN)	95	59.28	9.25	166	Gvarv 93
9 Kviteseid (SB)	300	59.40	8.47	320	Høydalsmo 560
10 Birkenes (BN)	150	58.36	8.22	236	Kjevik 12
11 Etne (SB)	200	59.70	5.95	162	Førde 64
12 Ullensvang (SB)	138	60.39	6.78	895	Ullensvang 12
13 Leikanger (SB)	138	61.15	6.72	352	Vangsnes 49
14 Norddal (SB)	125	62.33	7.31	244	Tingvoll gård 23
15 Rauma (SB)	138	62.57	7.58	357	Tingvoll gård 23
16 Melhus (SB)	63	63.24	10.23	208	Orkanger 4
17 Steinkjer (SB)	63	64.02	11.54	564	Melhus 63
18 Namdalseid (MB)	138	64.39	11.09	298	Steinkjer 63
19 Lierne (NB)	450	64.38	13.66	582	Nordli 433
20 Vefsn (MB)	200	65.76	13.26	441	Mosjøen 72
21 Målselv (NB)	125	69.11	18.65	447	Bardufoss 76
22 Lenvik (MB)	63	69.39	17.93	186	Tromsø 100



**Fig. 1.** Maps of Norway with county boundaries and the position of each study area from the two study periods. Study areas are numbered as in [Tables 1 and 2](#) Map base: Kartverket (Creative Common Attribution ShareAlike 3.0).

humidity than on forest stand age. Downy birch *Betula pubescens* dominates in the tree layer, and bilberry in the field layer. Another dominant species in all areas is the wavy hair-grass, but also several other grasses and sedges are common. Willows *Salix* spp. are often the dominating bushes, but in most of the areas also dwarf birch *Betula nana* and common juniper *Juniperus communis* are common. One study area (no. 2) is situated in mainly low productive old forest dominated partly by Norway spruce *Picea abies* and partly by Scots pine *Pinus sylvestris*, with bilberry and heather *Calluna vulgaris* as common species in the field layer and creeping willow *Salix repens* in the bush layer.

The three remaining study areas (no. 3–5) are situated in coniferous or mixed forests that are subject to commercial forestry, and which thus provide more habitats with grass and herbs, preferred by *Microtus* voles ([Wegge and Rolstad, 2018](#)), than does area 2. Scots pine, Norway spruce and birch *Betula* spp. are the most common tree species, and willows and juniper the most common bushes. Bilberry is a dominating species in the field layer of old forest stands. Grasses, in particular wavy

hair-grass, are common in clear-cuts. In two of the areas (no. 3 and 5), fixed trap sites were used throughout the study period, giving both grade-wise (successions) and step-wise (logging) changes in the field layer composition. In the third area (no. 4), voles were trapped in both old, bilberry-dominated forest and in grass-dominated clear-cuts; in the latter traps were moved periodically in order to maintain coverage of grassy sites. We regard the use of all trap sites from each of these three areas to give the best comparable result.

2.4. Summer temperature

For both study periods, the summer temperature indices used for each district or study area were the mean temperature in July (warmest month), in June–August and in May–September, taken from the closest meteorological station with data for the normal period 1961–1990 ([Tables 1 and 2](#)). The reason for using temperatures for the 1961–1990 normal period is that it was difficult to find stations close to each

**Table 2**  
Study areas in Norway where voles were snap-trapped each autumn during 1994–2015. Dominating vegetation zone ([Moen, 1999](#)) is given as BN = boreo-nemoral, SB = southern boreal, MB = middle boreal, NB = northern boreal, A = alpine. The meteorological station used for calculating altitude-adjusted summer temperature is given for each area. \* denotes study areas included in the terrestrial ecosystem monitoring programme ([Framstad, 2017](#)).

Study area	Mean altitude (m a.s.l.)	Latitude	Longitude	Number of voles trapped	Meteorological station and altitude (m a.s.l.)
1 Lund (MB)*	385	58.55	6.43	158	Eik 65
2 Solhomfjell (SB)*	312	58.95	8.83	845	Treungen 252
3 Ås (BN)	85	59.69	10.76	555	Ås 95
4 Varaldskogen (SB)	300	60.17	12.50	768	Roverud 150
5 Vangsåsen (MB)	575	60.94	11.14	1505	Ilseeng 182
6 Fuggdalen (MB)	710	61.78	11.30	323	Drevsjø 672
7 Gutulia (NB)*	812	62.03	12.16	111	Drevsjø 672
8 Åmotsdalen (NB)*	912	62.46	9.42	385	Sunnalsøra 10
9 Møsvatn (NB)*	1025	59.86	8.29	415	Møsvatn 977
10 Finse (A)	1250	60.60	7.50	59	Finse 1250
11 Heimdalen (NB)	1150	61.42	8.90	717	Dombås 638
12 Borgefjell (NB)*	550	65.06	13.81	182	Majavatn 319
13 Dividalen (NB)*	500	68.72	19.79	245	Dividalen 204

**Table 3**

Results from GLM models (Poisson distribution and log link, corrected for overdispersion) with the total number of *Microtus* voles captured in 22 study areas during 1971–1979 as response variable, the log-transformed number of trap nights as offset, and summer temperature, snow depth on 1 April and the proportion of fields as predictors. A, B and C represent use of different temperature variables in the models.

Explanatory variable	Estimate	SE	df	$\chi^2$	p-value
A)					
Intercept	−0.6058	1.7372			
Snow April	0.0087	0.0042	1	4.54	0.0331
Temperature July	−0.2530	0.1283	1	4.16	0.0415
Proportion fields	0.0174	0.0059	1	8.36	0.0038
B)					
Intercept	−0.2853	1.6336			
Snow April	0.0065	0.0044	1	2.18	0.1397
Temperature June–August	−0.2852	0.1243	1	5.64	0.0175
Proportion fields	0.0167	0.0055	1	8.91	0.0028
C)					
Intercept	−0.3817	1.5251			
Snow April	0.0041	0.0051	1	0.65	0.4192
Temperature May–September	−0.3115	0.1298	1	6.20	0.0128
Proportion fields	0.0156	0.0052	1	8.48	0.0036

district (1971–1979) or study area (1994–2015) that were active throughout the specific study period. There has been a general temperature increase in Norway, but less in summer than in winter. When comparing the 30-yr period 1978–2008 with the normal period 1961–1990, the mean winter temperature increased by about 1 °C, whereas the summer temperature only increased with 0.3–0.4 °C (Official Norwegian Reports, 2010). The spatial variation seems to be minor; during 1900–2014, the mean increase in summer temperature per decade varied from 0.05 to 0.08 °C between the six Norwegian temperature regions (Hanssen-Bauer et al., 2017).

We adjusted for altitude difference between the available meteorological stations and the study regions or areas by assuming a temperature lapse rate of 0.67 °C per 100 m elevation (Høiland et al., 2005; Trigo et al., 2010).

## 2.5. Snow conditions

As an index of snow conditions for each study area, we used the average of the annual estimated snow depth on 1 April for the study period in question (1971–1979 or 1994–2015), and not from the normal period (1961–1990), because for this factor we expect a direct effect on vole performance. We assume that there is a strong correlation between this index and the duration of the period with snow cover, and that areas that usually have a thick snow cover in April usually also provide favourable snow conditions for voles throughout winter.

By clicking at a point on a digital map of Norway ([www.senorge.no](http://www.senorge.no)), the estimated snow depth at the selected date for that location is given, as well as the elevation for which the estimate is based. It was not possible to obtain an estimate for an elevation exactly equal to the mean altitude of each study area; the mean deviation was 16.3 m (range 1.5–65 m), with the highest deviations for the highest altitudes.

For the 22 areas trapped during 1971–1979, the snow depth on 1 April was positively related to altitude ( $P = 0.002$ ) and longitude ( $P < 0.001$ , Total  $R^2 = 0.71$ ), whereas for the 13 areas trapped during 1994–2015, snow depth on 1 April was related to altitude only ( $p = 0.002$ ,  $R^2 = 0.61$ ). The only summer temperature index that was not significantly correlated with the snow depth index was mean July temperature for the 22 areas trapped in 1971–1979 ( $r = -0.34$ ,  $p = 0.13$ ).

## 2.6. Statistical analyses

For the period 1971–1979, when the same trapping design was used in all study areas, we used the number of *Microtus* voles and *Myodes* voles trapped as response variables in GLM models (Poisson distribution and log link, corrected for overdispersion), with the log-transformed number of trap nights as offset. The explanatory variables were snow cover (snow depth April 1), three temperature indices and the proportion of fields, which we expected to have highest population levels of *Microtus* voles (Hansson, 1978). We did not conduct a similar analysis for the period 1994–2015, because the data from the different study sites were not directly comparable due to different trapping design. Instead, we used the proportion of *Microtus* voles in the total vole captures from each study area or district, and included also the data from 1971 to 1979 (total  $n = 35$ ), as response variable in GLM models (binomial distribution and logit link). The explanatory variables were snow cover (snow depth April 1), three temperature indices and study period (dummy variable). We also tested for interactions between study period and the temperature indices. The software used was JMP<sup>®</sup> Pro 12.1.0 (SAS Institute, Cary, North Carolina).

## 3. Results

The number of *Microtus* voles captured in the 22 districts during 1971–1979 correlated negatively with summer temperatures and positively with the mean proportion of the area of abandoned fields in multivariate models with the log-transformed number of trap nights as offset (Table 3). When using only the mean July temperature as an index for summer temperatures, there also was a significant positive relationship with snow depth (Table 3). The relationship with the climate variables was significant also in univariate tests, whereas the relationship with abandoned fields was not ( $\chi^2 = 1.46$ ,  $p = 0.23$ ). The best single predictor of the number of *Microtus* voles trapped was the temperature in May–September ( $\chi^2 = 8.55$ ,  $p = 0.004$ ).

The number of *Myodes* voles trapped varied less between the 22 districts than did that of *Microtus* voles, and was not significantly related to any of the selected explanatory variables, neither in multiple ( $p > 0.4$ ) nor in univariate models ( $p > 0.2$ ). The grey-sided vole, which is the most *Microtus*-like of the three *Myodes* species, occurred in only six of the 22 districts, but excluding it from the data set did not affect the results. The number trapped of this species was, however, positively related to the proportion of fields ( $\chi^2 = 9.46$ ,  $p = 0.002$ ) and negatively related to May–September temperature ( $\chi^2 = 6.17$ ,  $p = 0.013$ ), just as the number of *Microtus* voles was. Both variables contributed significantly in a multiple model (fields:  $\chi^2 = 37.38$ ,  $p < 0.001$ ; temperature:  $\chi^2 = 34.93$ ,  $p < 0.001$ ).

The proportion of *Microtus* voles among voles captured was negatively related to summer temperatures and positively related to snow depth in multivariate models, regardless of the summer temperature index used (Table 4; Figs. 2 and 3), and whether or not the grey-sided vole was excluded from the samples. In addition, there was a significant effect of study period, because the *Microtus* vole proportion in general was higher in the first period than in the second (Figs. 2 and 3). The interaction between study period and temperature indices was not significant. When the two periods were analysed separately, the snow index contributed with a positive effect only in the first period, in contrast to the summer temperature indices, which had a negative effect in both periods. In univariate analyses, the proportion of *Microtus* voles among voles captured correlated significantly with all climate variables in both periods, with temperature in May–September as the best predictor.

## 4. Discussion

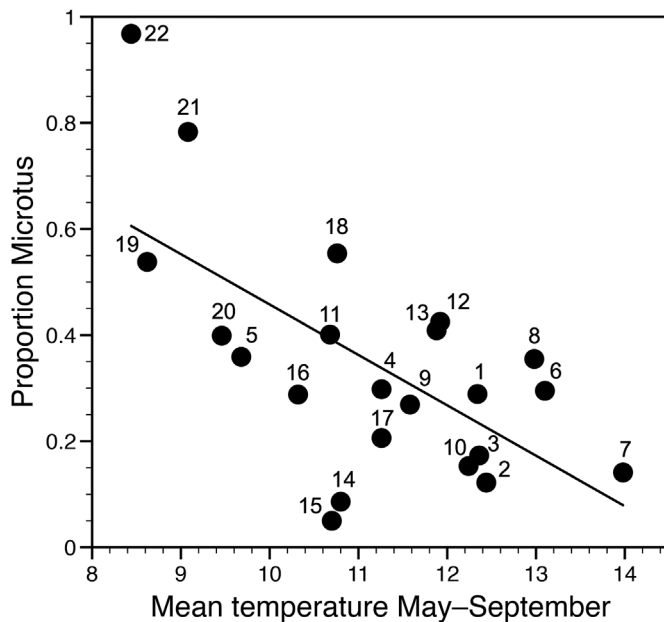
Both for the number of *Microtus* voles trapped in 1971–1979, and for the proportion of *Microtus* voles in the total vole capture from both



**Table 4**

Results from GLM models (binomial distribution and logit link) with the proportion of *Microtus* voles in vole captures (*Microtus* and *Myodes* pooled) as response variable and summer temperature, snow depth on 1 April and study period as predictors, for 22 areas trapped in 1971–1979 and 13 areas trapped in 1994–2015. A, B and C represent use of different temperature variables in the models.

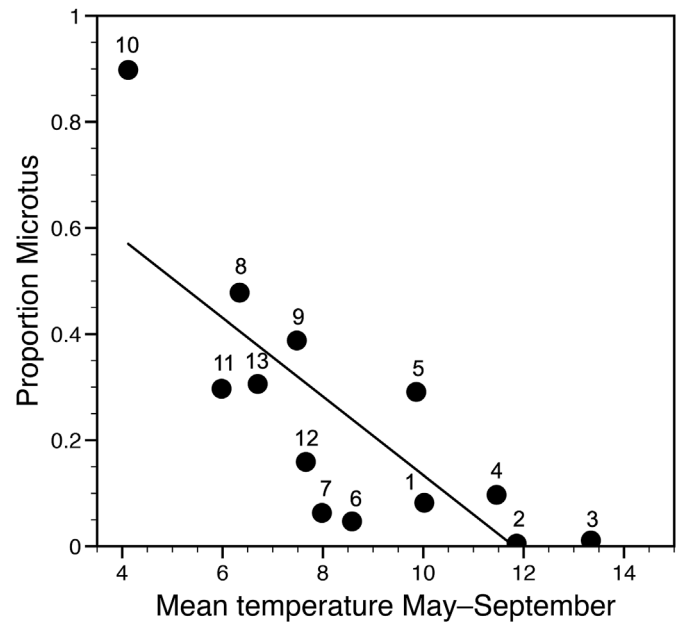
Explanatory variable	Estimate	SE	df	$\chi^2$	p-value
A)					
Intercept	1.7754	0.2040			
Snow April	0.0074	0.0007	1	97.45	< 0.0001
Temperature July	−0.2456	0.0144	1	297.55	< 0.0001
Period	0.7148	0.0246	1	970.09	< 0.0001
B)					
Intercept	2.1919	0.2060			
Snow April	0.0053	0.0008	1	45.03	< 0.0001
Temperature June–August	−0.2883	0.0153	1	365.08	< 0.0001
Period	0.7393	0.0250	1	1016.83	< 0.0001
C)					
Intercept	2.2131	0.1961			
Snow April	0.0026	0.0009	1	9.54	0.0020
Temperature May–September	−0.3330	0.0167	1	411.45	< 0.0001
Period	0.7766	0.0257	1	1072.32	< 0.0001



**Fig. 2.** The proportion of *Microtus* voles among voles captured (*Microtus* and *Myodes* pooled) in Norway 1971–1979 in relation to mean temperature in May–September in each study area. Study areas are numbered as in Table 1 and Fig. 1a.

study periods, May–September temperature was a better predictor than snow depth in early April. For the second study period 1994–2015, when vole cycles in general were less pronounced than during 1971–1979 (Cornulier et al., 2013), better correlation with summer temperature than with snow cover was particularly evident. A decrease in forage quality would be expected with increasing summer temperatures and an extended growing season (Jonasson et al., 1986; Laine and Henttonen, 1987). If regular herbivore outbreaks mainly reflect stress-induced and climate-synchronized increases in protein digestibility of common food plants (White, 1993, 2011; Selås, 2016b), increasing summer temperatures should be unfavourable also by reducing the time needed by plants to recover after a stress event, such as a high seed crop (White, 1984).

In the multiple analyses of the proportion of *Microtus* voles, we also



**Fig. 3.** The proportion of *Microtus* voles among voles captured (*Microtus* and *Myodes* pooled) in Norway 1994–2015 in relation to mean temperature in May–September in each study area. Study areas are numbered as in Table 2 and Fig. 1b.

found a significant difference between the two study periods, with generally higher *Microtus* vole proportions in 1971–1979 than in 1994–2015. The main reason for this is probably that Christiansen (1983) selected study sites that were good habitats for *Microtus* voles. Particularly in areas with a high proportion of abandoned fields, the number of *Microtus* voles was high. Such habitats provide both preferred food plants and shelter, with soil types well suited for burrowing (Hansson, 1978). However, also a general temperature increase from the 1970s to the present may have contributed to the observed difference between the study periods. We did not correct for this temperature increase in our analyses but used the same normal period (1961–1990) when calculating elevation-adjusted summer temperatures for each study area or region. Snow indices, on the other hand, were calculated for each specific period, and should thus not be biased by climate change.

Although the number of *Myodes* voles trapped during 1971–1979 was not related to summer temperature on a spatial scale, a negative relationship was found on a temporal scale for population indices of bank vole from post-mast years of bilberry in southern Norway during 1980–2008 (Selås et al., 2011a). A negative relationship between summer temperatures and herbivore number or performance has been found also for several other taxa, including moths (Selås, 2000; Johnson et al., 2010), grouse (Selås, 2000; Selås et al., 2011a), hares (Scott and Craine, 1993; Yan et al., 2013; Bisi et al., 2015) and cervids (Selås et al., 2011b). What these herbivores have in common is that they feed on perennial plants with variable seed production at higher altitudes or latitudes. Variable snow cover is not likely to be the common link between climate and the population performance of these animals. Snow is advantageous for voles, and possibly advantageous for hares, which are better adapted to run on snow surfaces than most mammalian predators, but hardly for the moth, grouse or cervid species in question.

In spite of the evidence for summer temperatures as an important factor for *Microtus* vole populations, we actually found an additional statistical effect of snow cover in the multiple regression models, and in particular when using only July temperature, which was the only summer temperature index not significantly correlated with the snow index. A late snowmelt shortens the length of the growing season, and may thus favour the herbivorous *Microtus* voles, regardless of

midsummer temperatures. *Myodes* voles, on the other hand, are probably positively affected by an early spring thaw, due to the benefit of access to animal proteins (arthropods) for their reproduction (Von Blanckenhagen et al., 2007).

A permanent snow cover throughout winter may also be more favourable for *Microtus* voles than *Myodes* voles, for two reasons. Firstly, *Microtus* voles seem to spend less time upon the snow than do *Myodes* voles (Sonerud, 1986; Nybo and Sonerud, 1990; Jacobsen and Sonerud, 1993) and may thus experience relatively lower predation risk when the ground is covered by snow. Secondly, any dependence on favourable snow conditions for reproduction during winter (Duchesne et al., 2011) should mainly affect the population dynamic of *Microtus* voles, which in contrast to *Myodes* voles also reproduce in winter during the increase phase of the population cycle (Larsson et al., 1973; Eriksson, 1984; Hansson, 1984). Unfavourable snow conditions, caused by melting and freezing, are most likely to occur in lowland areas with oceanic climate, and may thus have contributed to the low *Microtus* proportion in area 14 and 15 in the first study period. However, in the second study period, unfavourable snow conditions were observed for several years in the most alpine study area, Finse (Kausrud et al., 2008), where the proportion of *Microtus* voles actually was highest.

We have not analysed for temporal relationships with summer temperature. The main reason is that we lack data on seed production of important food plants, which we regard as a key factor for annual fluctuations in rodent numbers in Norway (Selås, 1997, 2016b), and which should be controlled for in temporal analyses. Populations of *Microtus* and *Myodes* voles do not always fluctuate in synchrony (Framstad, 2017), possibly because different food plant species respond somewhat differently to weather variables responsible for synchronizing intraspecific flowering. Hence, for temporal analyses, also better knowledge of the impact of temperatures on key stages of the flowering cycle of each food plant species may be needed.

Finally, it is worth to mention that increasing temperatures also reduce surface cosmic ray fluxes (De Mendonca et al., 2013), which may thus be an integral part of the temperature effects on plant resistance against grazing. A support for the hypothesis of an indirect effect of cosmic rays on herbivores is that the mean cycle period of several herbivore species corresponds to the periodicity of the 11-year solar cycle or the 9.3-year lunar nodal phase cycle (Klvana et al., 2004; Archibald, 2014; Selås, 2014), the two main modulating factors for surface cosmic ray fluxes. The 9.3-year lunar signal is evident even in two time series of bilberry seed crops from Norway (Selås et al., 2015). Although the impact of snow should not be ignored, our conclusion is that further studies of vole population dynamics need to focus on conditions during the growing season that affect the vole food plants, in particular summer temperatures.

## Author contributions

VS formulated the idea, all authors contributed with data, VS analysed the data and wrote the manuscript, other authors provided editorial advice.

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